Evolutionary adaptations of temperature regulation in mammals[1]

By L. Jansky

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Generally speaking, adaptations may take place either during individual life of animals (acclimations and acclimatizations), or they may be specific to certain species (evolutionary adaptations) (Hart 1963b). They may be realized by different mechanisms with different degree of efficiency, however the aim of all adaptations is essentially the same — to reduce the dependence of animals on environmental conditions and thus to increase their ecological emancipation. The study of physiological mechanisms of adaptations is therefore of great ecological importance since it helps us to elucidate physiological processes influencing limits of distribution of different species and having a profound effect on the quality or density of animal populations. The comparison of individual and evolutionary adaptations permits us to trace the evolutionary progressive physiological processes and to contribute to the problems of phylogeny.

In lowered temperatures mammels tend to lose heat. Theoretically, they can prevent hypothermia either by increasing heat production in the body or by reducing heat loss from the body to the environment. Heat production is realized by shivering; heat conservation may be manifested by reducing the body surface, by improving its insulation qualities and by decreasing the body—air temperature gradient according to formula:

$$H = K \frac{T_B - T_A}{I} \quad (1) \qquad \text{(Hart, 1963b)}$$

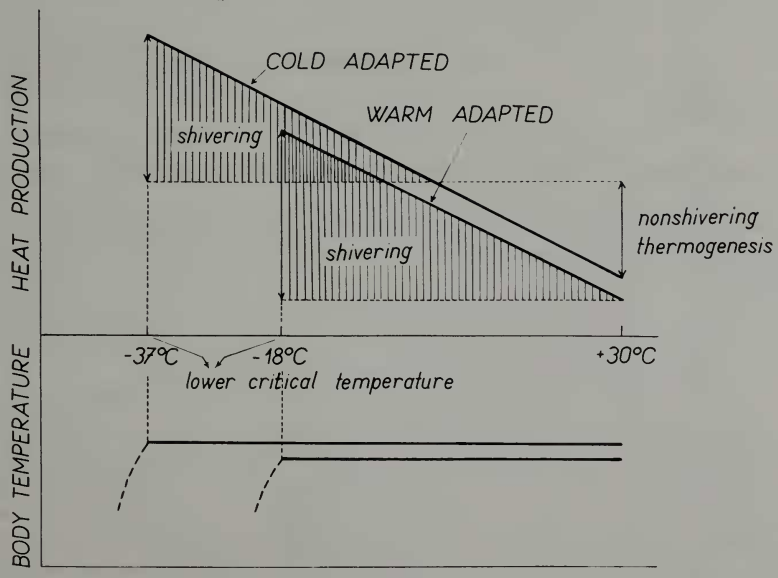

Fig. 1. Scheme of heat production of rats adapted to warm (30° C) and cold (5° C) environments. According to Hart & Jansky, 1963

[1] Presented at the 40th meeting of the German Mammalogical Society in Amsterdam.

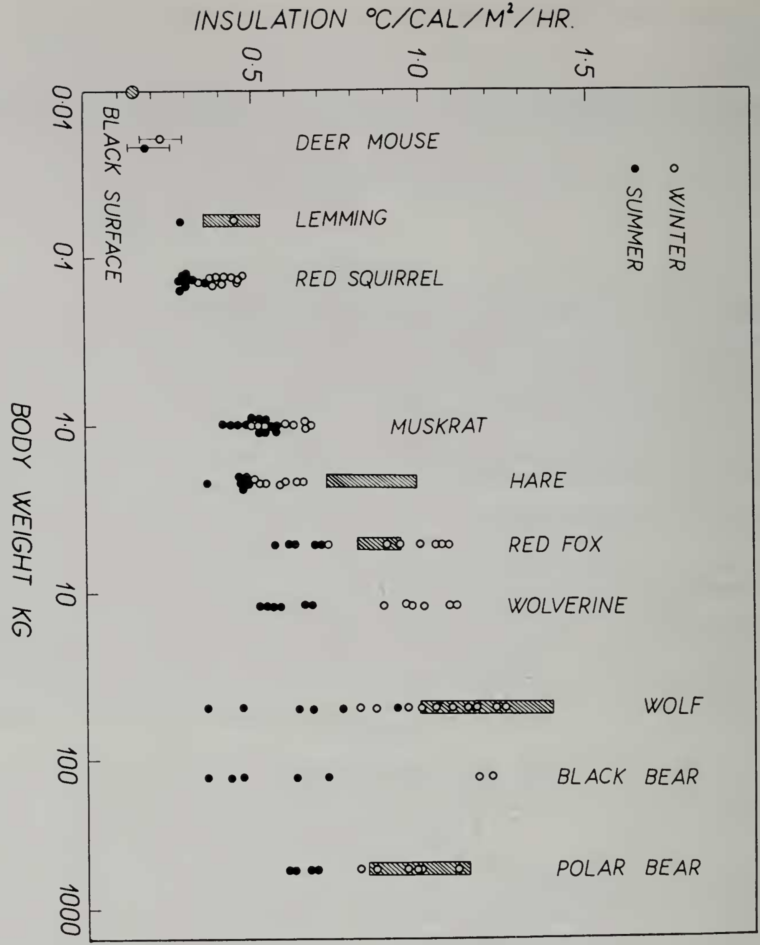

Fig. 2. Seasonal changes in fur insulation in various mammals (Hart, 1956)

(H = heat production, K = a constant representing the body surface area, T_B = body temperature, T_A = air temperature, I = insulation qualities of the body surface.)

Similary, the adaptations of temperature regulation to cold can be realized either by increasing the capacity of heat production or by mechanisms leading to reduction of heat loss from the body. The adaptation to cold appears as a shift of the lowest temperature limit animals can survive (lower critical temperature).

In our earlier work we have shown that the individual adaptations are manifested predominantly by an increased capacity of heat production owing to the development of a new thermogenetic mechanism — called nonshivering thermogenesis (Hart, Jansky 1963). Physiological background of this phenomenon consists in an acquired sensitivity of muscular tissue to thermogenetic action of noradrenaline liberated from sympathetic nervous endings (Hsieh, Carlson 1957). Nonshivering thermogenesis potentiates heat production from shivering and in rats shifts the lower critical temperature for about 20° C (from −18° C down to — 37° C; Fig. 1).

Mechanisms controlling heat loss by changes in body surface area or by changes in body-air temperature gradient are not common in individual adaptations. On the other hand it is well known, that certain species can improve body insulation in winter season. However, this phenomenon becomes functionally justified only in animals of greater size (size of fox and larger; Fig. 2. HART 1956).

The individual adjustments with the aid of nonshivering thermogenesis are encountered both in acclimations under laboratory conditions and in seasonal acclimatizations induced in the same species under natural conditions. They are undoubtelly very efficient and biologically important. On the other hand, from the ecological point of view, they have also their negative side. The increased heat production results in higher demands for energy restitution in the body, which is attained in cold adapted animals by an increased food consumption. As a result, individuals adjusted this way become more dependent on the quantity and availability of food and they are forced to use more effort to provide it. The reduced dependence of animals on temperature factors is thus substituted by increased dependence on food factors.

Contrary to individual adaptations, in evolutionary adaptations mechanisms leading to the reduction of the heat loss are greatly emphasized. Their importance consists in the fact that they save energy for the organism and have lower demands to its restitution in the body. This fact is obviously evolutionary very important — in the processes of phylogeny there occurs natural selection of those individuals that are less impeded by the lack of food, often occuring in nature.

Evolutionary adaptations are realized in the first place by an increased insulation of the body cover (fur, Fig. 3). This adjustment, typical for arctic animals, can reduce the heat loss so efficiently, that even considerably reduced ambient temperatures (down to — 50° C) do not result in an increased heat production in larger animals. (Fig. 4; SCHOLANDER et al. 1950a, b). The same role plays a thick layer of subcutaneous fat which appears in some mammals, such as seal and swine. The insulation qualities of this fat layer can be increased by an active restriction of the blood flow to this area. This results in superficial hypothermia, which also efficiently prevents the heat loss (IRVING 1956). Animals endowed with superficial hypothermia have normal thermogenetic abilities. However, compared to the species from tropical regions with little insulation and to arctic species with great surface insulation they show a reduced sensitivity of afferent sensory input to temperature stimuli (Fig. 5).

A tendency to reduce heat loss by reduction of the body surface area may be considered as another type of evolutionary adaptations. This phenomenon occurs in animals living permanently in cold climate, which are generally larger and have shorter body appendages than animals from tropical zone (BERGMANN's and ALLEN's rules). Both the validity and the physiological significance of these rules have been recently questionend by several workers, however.

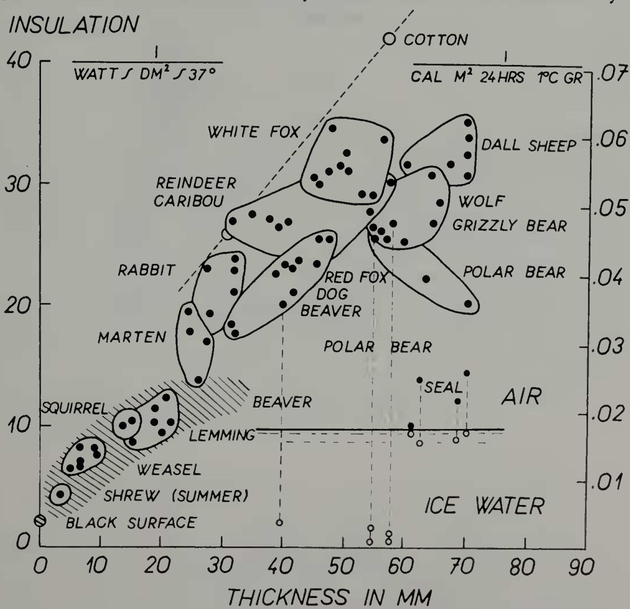

Fig. 3. Insulation in relation to winter fur thickness in arctic and tropical mammals (SCHOLANDER et all., 1950 b)

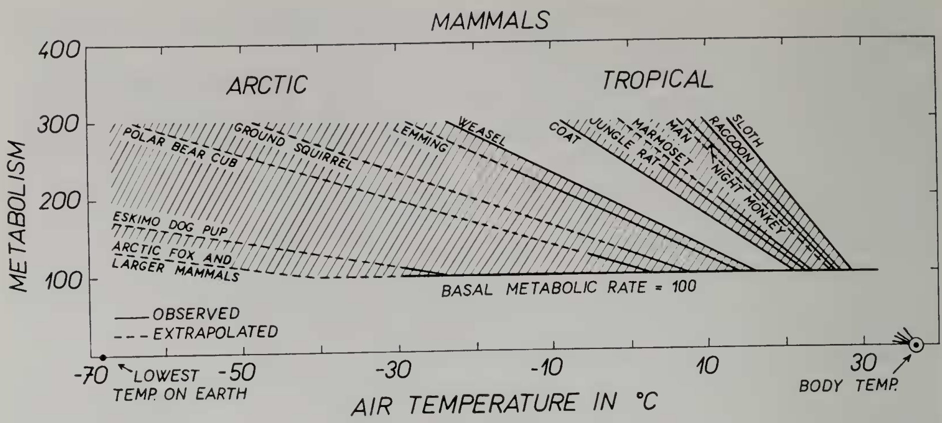

Fig. 4. The effect of environmental temperature on metabolism of arctic and tropical mammals (Scholander et all., 1950 a)

The reduction of heat loss by changing the body-air temperature gradient can be realized either by active choice of higher environmental temperature or by considerable lowering of body temperature.

It is generally recognized that the active choice of the environmental temperature occurs by seasonal migrations and by changes in patterns of daily activity. It was found that different species of voles and shrews transfer the peak of daily activity to warmer part of the day in a cold weather (Jansky & Hanák 1959).

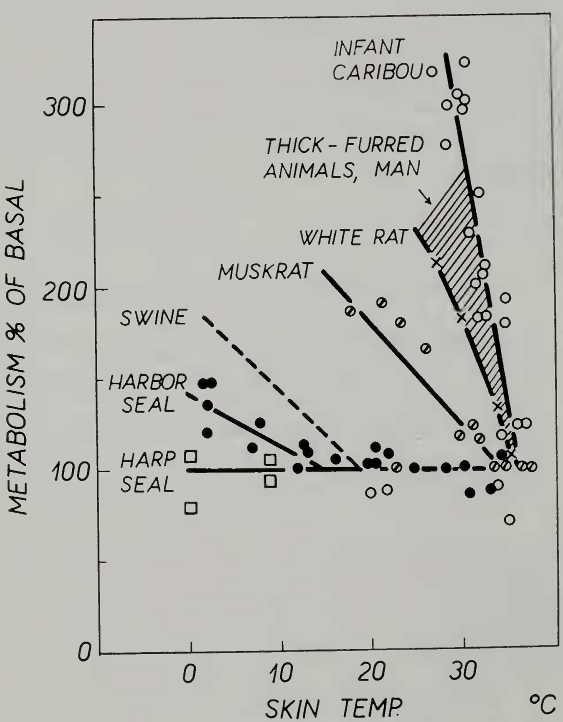

Fig. 5. Heat production as a function of skin temperature under fur of the back for a series of mammals (Hart, 1963 a)

The mechanisms leading to reduction of body-air temperature gradient by lowering of body temperature are especially developed in hibernators. According to the latest view hibernation is not considered as a lack of temperature regulation rather as a special adaptation of thermogenetic processes. There are two reasons for that: first, hibernators have the same capacity of heat production as other hemeotherms of similar size (see Jansky, 1965) and second, the entering, the arousal and the deep hibernation are under remarkably precise physiological control (see Lyman, 1963).

This indicates a leading role of central nervous system in controlling hibernation, which is adapted to hypothermal conditions and it is functional at all levels of body temperature. This adaption has certainly its metabolic background, however only little is known about this phenomenon so far.

The control of entering into hibernation is realized by the active inhibition of shivering heat production by signals from subcortical centres of the brain. Simultaneously with the decrease in shivering an active inhibition of the activity of the sympathetic nervous system also takes place, which is manifested by the reduction of heart rate and by vasodilatation. These changes facilitate the lowering of body temperature of animals which is realized successively in the form of "undulating" cooling so the organism can slowly prepare to hypothermia (Fig. 6). Nervous control of hibernation persists in deep hypothermia as evident from the sensitivity to thermal and other stimuli. The arousal from hibernation is equally an active process, very efficiently controlled, so that organism can produce a great amount of heat in minimum of time. The coordination of thermogenetic processes depends also on the activity of nervous centres. Characteristic of awakening is the preponderence of sympathetic nervous system, leading to vasoconstriction and to an increase in heart rate. The main source of heat in awakening is again constituted by shivering. However, nonshivering heat production was also found during arousal and also the rapidly beating heart, working against a high pressure, may contribute a certain amount of heat.

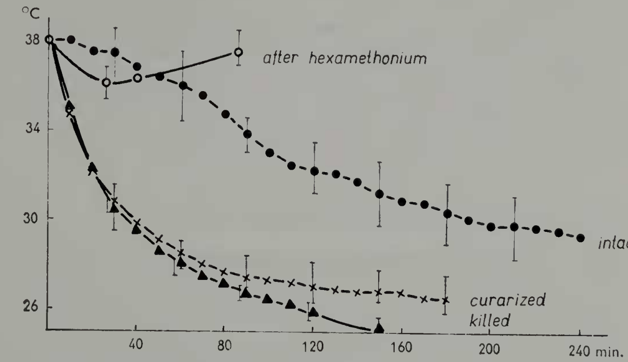

Fig. 6. Changes in body temperature of the bat *Myotis myotis* during entering hibernation (Jansky, Hájek, 1961)

Summary

On the basis of all mentioned data we conclude that the adaptations of temperature regulation to cold may be realized either by an increased ability to produce heat or by reducing the heat loss. While the individual adaptations are manifested chiefly metabolically as evident from an increased capacity of heat production, the inherited adaptations are realized mainly by mechanisms leading to the heat loss reduction (e. g. increased insulation by fur or by superficial hypothermia, reduction of body surface area, active choice of environmental temperature and lowering the body temperature). The control of the mentioned adjustments consists in the changes in function of the central and sympathetic nervous systems inducing changes in intensity of the energy metabolism (individual adaptations), changes in the plasticity of vasomotor mechanisms and in heat production of hibernators during entering into and awakening from hibernation (evolutionary adaptations). Morphologically based adjustments (improvement of insulation by fur) appearing in both evolutionary and individual adaptations forms the connecting link between both types of adaptations.

Zusammenfassung

Aus allen erwähnten Daten folgern wir, daß die Adaptationen der Temperaturregulierung bei Kälte entweder durch die erhöhte Wärmeproduktion oder durch die Verringerung des Wärmeverlustes erreicht werden. Während die individuellen Adaptationen hauptsächlich metabolischer Art sind, was durch die erhöhte Kapazität der Wärmeproduktion in Erscheinung tritt, findet man erbliche Adaptationen zumeist in Form von Mechanismen, die eine Verringerung des Wärmeverlustes bewirken (z. B. erhöhte Isolierung durch das Fell oder durch oberflächliche

Hypothermie, Verringerung der Körperoberfläche, aktive Wahl der Umgebungstemperatur und Absinken der Körpertemperatur). Die Steuerung der erwähnten Anpassungen beruht auf Veränderungen in der Funktion des zentralen und des sympathischen Nervensystems, welche Veränderungen in der Intensität des Energiestoffwechsels (individuelle Adaptationen) hervorrufen, weiterhin Veränderungen in der Plastizität der vasomotorischen Mechanismen und in der Wärmeproduktion von Winterschläfern beim Einritt in den Winterschlaf und beim Erwachen (evolutive Adaptationen). Morphologische Adaptationen (Verbesserung der Isolierung durch das Fell), die sowohl als evolutive und auch als individuelle Adaptationen vorkommen, stellen die Verbindung zwischen beiden Typen der Adaptation her.

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Die Wurfzeit des Waldlemmings, *Myopus schisticolor* (Lilljeborg, 1844)

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Da systematische Erhebungen über die Wurfzeit von Kleinsäugern, aber auch der übrigen Wildsäuger, weitgehend fehlen, wurde diesem Gesichtspunkt in der Oldenburger *Myopus*-Zucht besondere Aufmerksamkeit geschenkt. Von 193 zeitlich erfaßten Geburten erfolgten 103 (= 53,4 %) in der Zeit von 0 bis 8 Uhr, 59 (= 30,6 %) von 8 bis 16 Uhr und 31 (= 16 %) von 16 bis 24 Uhr. Ebenso wie beim Menschen (Hosemann 1946) konnte kein exogener Einfluß auf die Geburtszeit festgestellt werden. Diese